MANAGEMENT AND RESTORATION ECOLOGY OF THE FEDERAL THREATENED MEAD'S MILKWEED, *ASCLEPIAS MEADII* (ASCLEPIADACEAE)[1]

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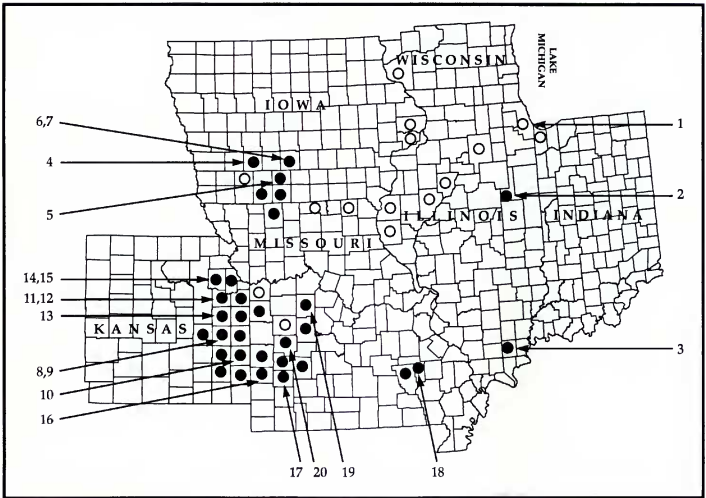
ABSTRACT

The federal threatened *Asclepias meadii* Torr. (Asclepiadaceae) is a perennial, self-incompatible prairie forb imperiled by habitat destruction and population fragmentation. Many large populations persist in prairie haymeadows in Kansas and Missouri despite removal of seed pods by annual summer mowing. Only a few small populations remain in Illinois, Iowa, and northern Missouri. Recovery of these small populations and restoration of new populations are recovery objectives for this species. This study was conducted to determine habitat differences among populations, to understand how hay mowing and fire management affect the structure of *A. meadii* populations, and to test the effects of different management treatments on restoration of this species. Soils analysis showed a geographic gradient, with southern populations on acid, nutrient-poor soils, and northern populations on calcareous, nutrient-rich soils. Milkweed ramet densities were lower in fire-managed prairies than in haymeadows; but burned sites had 68% flowering ramets while haymeadows had only 19% flowering ramets. This suggests that burning has selected for greater resource allocation toward sexual reproduction, while annual hay mowing has selected for greater resource allocation toward clonal spread. The Morton Arboretum is conducting experimental restoration of *Asclepias meadii* in the eastern part of its range, an objective of Federal Recovery Planning. In greenhouse and garden experiments, competition from oats significantly reduced seedling growth, with greater growth in artificially outcrossed seedlings. At seven restoration sites in Illinois and northern Indiana, significant variation in milkweed germination, survivorship, and growth was caused by weather, differences among sites, and site management. Seedlings were vulnerable to drought, with greater survivorship when rainfall was 200% of normal. Planted juvenile milkweeds had greater survivorship than seedlings, and less sensitivity to drought. Greater growth and survivorship also occurred in burned than in unburned plots at three sites, but not in all life-stages. Propagated plants from Missouri seed sources were larger than Kansas plants in the garden, but not in the field. Continued work is needed to determine if restored populations can become viable, and if there are negative effects of crossing and translocating genotypes.

Managing for viable populations of endangered species requires knowledge of their life-history and habitat requirements, reproductive biology, and the demographic, genetic, and ecological traits that make them vulnerable to extinction processes (Gilpin & Soulé, 1986; Lande, 1988; Menges, 1986, 1991, 1992). Similar information is required to recover and restore new populations of these species, especially how site-management and stochastic environmental processes affect population growth based on their genetic attributes, reproductive characteristics, and survivorship at different life

history stages (Fenster & Dudash, 1994; Weller, 1994; Pavlik, 1994, 1996; Guerrant, 1996). This paper examines factors that affect the management and restoration ecology of Mead's milkweed (*Asclepias meadii* Torr., Asclepiadaceae), a federal threatened (Harrison, 1988) plant essentially restricted to the virgin tallgrass prairies of the midwestern United States (Betz, 1989). To better understand how to manage and restore this species, we compare habitat characteristics across its range, examine the effects of management on population structure, and use experimental propagation and

Site Number, Name & State

1 Palatine, IL	6 Cummings, IA	11 Colyer, KS	16 Cook Meadow, MO
2 Ford, IL	7 Martensdale, IA	12 Jack's, KS	17 Niawathe, MO
3 Saline, IL	8 Garnett, KS	13 Flower Hill, KS	18 Weimer Hill, MO
4 Woodside, IA	9 Sunset, KS	14 French Creek, KS	19 Paint Brush, MO
5 Flaherty, IA	10 Hinton Creek, KS	15 Rockefeller, KS	20 Wah-kon-Ta, MO

Figure 1. Distribution by county of *Asclepias meadii*. Closed circles are counties with extant populations; open circles are counties from which populations have been extirpated. Study site locations are numbered corresponding to Table 1.

restoration to understand the effects of environmental variation and site management on population establishment.

DISTRIBUTION AND STATUS

The range of *Asclepias meadii* follows the tallgrass prairie, extending eastward from Kansas through Missouri, Iowa, and Illinois to southwestern Wisconsin and northwestern Indiana (Fig. 1). Because of conversion of tallgrass prairie to agriculture, *A. meadii* has been reduced to about 150 populations, primarily in Kansas and western Missouri native haymeadows. These haymeadows are usually summer-mowed, which removes milkweed pods (follicles), preventing seed dispersal and sexual re-

production (McGregor, 1977; Betz, 1989). Hay mowing has occurred almost annually for a century (Fitch & Hall, 1978), yet many haymeadows contain hundreds of milkweed ramets. One former haymeadow, the Rockefeller Prairie, Jefferson Co., Kansas, has been fire-managed since the 1950s and may contain 200 or more plants (Alexander et al., 1997). Less than 20 former haymeadow populations have been preserved as public prairies in Missouri since the mid 1980s, and only one site contains a large population (Smith, 1997). A metapopulation of *A. meadii* occurs across a complex of non-mowed igneous glades in southeast Iron and Reynolds Cos., Missouri. The largest of these population groups has more than 100 plants and occurs at the

Figure 2. Flowering umbel and follicle of Mead's milkweed (*Asclepias meadii*). Reprinted with permission from *Erigenia* (Journal of the Illinois Native Plant Society); drawing by Nancy Hart Stieber.

fire-managed Weimer Hill site in Iron Co. Eastward, small colonies occur at two sites in northern Missouri, six Iowa sites, and five sites in Illinois; populations are extirpated from Wisconsin and Indiana (Betz, 1989; M. L. Bowles, pers. obs.).

BIOLOGY

Asclepias meadii (Fig. 2) is a long-lived rhizomatous perennial herb. As in many prairie plants, dormant season fire appears to stimulate flowering (Betz, 1989; H. M. Alexander, pers. comm.). Mature plants usually have 6–12 paired leaves and a single terminal umbel with about 12 flowers and usually produce a single narrow pod (per plant) with about 60 seeds (Betz, 1989). Flowers within an umbel are open for about 5–6 days, and flowering occurs for about 10–12 days within populations. Plants flower

as early as late May in the south through mid to late June in the north, depending upon yearly growing season conditions. Pollinia are most frequently removed by miner bees (*Anthophora* sp.), or by small bumblebees (*Bombus* sp.) (Betz et al., 1994). In a seven-year study, 77% of over 100 *A. meadii* ramets flowered annually, but less than 6.4% matured pods, averaging 61 seeds/pod and 47.6% seed germination (Betz, 1989). This correlates with low levels of pod production reported for most milkweeds (Wyatt, 1976), in which reproduction is regulated by their breeding system and by resource allocation (Willson & Price, 1980). Most milkweed species are self-incompatible, requiring crosses between genetically different individuals to produce viable seeds (Kephart, 1981; Shannon & Wyatt, 1986; Kahn & Morse, 1991; Broyles & Wyatt,

1991, 1993; Wyatt & Broyles, 1994). The apparent longevity of *A. meadii* and its restriction to virgin prairies suggests that it is a late-successional species characterized by poor colonizing but good competitive abilities. As a result, seedling establishment may be infrequent but is probably required for long-term population maintenance and necessary for population establishment. As yet, little experimental information is available about seedling ecology (Betz, 1989).

Asclepias meadii is genetically diverse, with 74% of its allozyme diversity maintained within populations or metapopulations and no geographic genetic pattern among populations (Tecic et al., 1998). Allozyme samples from the Rockefeller and Weimer Hill populations have found 15 or more genotypes per site, with small ramet : genet ratios, while haymeadows and small populations are highly clonal, with fewer genotypes and large ramet : genet ratios (Tecic et al., 1998). Formerly widespread species with outcrossing breeding systems become vulnerable to extinction because of lowered reproductive potential in fragmented populations (Schaal et al., 1991; Weller, 1994; Les et al., 1991; DeMauro, 1993). Such is the case for *A. meadii*. Because of its self-incompatible breeding system, small fragmented populations that are reduced to single clones, such as in Illinois, no longer produce seeds and are vulnerable to stochastic extinction processes. Viable restored populations of self-incompatible species should contain high levels of genetic diversity, which will enhance outcrossing and seed production while lowering inbreeding (DeMauro, 1993). For *A. meadii*, this may require infusion of large numbers of different genotypes from across the range of the species. Such efforts would maximize evolutionary potential and decrease inbreeding, but could alter historic lineages and produce outbreeding depression if co-adapted gene complexes exist and are disrupted (Fenster & Dudash, 1994). This issue is often contentious for restoration ecologists and will only be resolved with case-by-case experimentation among different plant groups (Bowles & Whelan, 1994).

Ex-situ Conservation

To facilitate recovery of *Asclepias meadii*, The Morton Arboretum has assembled a genetically diverse garden population and nursery to provide a propagule source for population restoration and research. The garden environment consists of 1 × 2-m elevated beds filled to 0.3 m with wood chips, in which potted milkweeds are propagated. The pots allow isolation of plants and removal for artificial cross-pollination. Seed sources have included extant populations and herbarium specimens representing western Missouri and Kansas (Bowles et al., 1993a). Important seed sources have included the Rockefeller Prairie and Weimer Hill, which have been supplemented by pollen crosses from fragmented eastern populations in southern (Saline Co.) and central (Ford Co.) Illinois, northern Missouri (Harrison Co.), and southern Iowa (Adair Co.). By 1996, the garden population contained 58 adult plants representing 28 different genotypes.

Objectives

Our objectives were to analyze ecological factors affecting the distribution, population structure, and restoration of *Asclepias meadii*. In this paper, we first examine the distribution of *A. meadii* in relation to soil characteristics, which, based on the lack of a strong geographic genetic pattern in this species, might be expected to show little variation. We also compare its population structure under regimes of hay mowing and burning, the primary management alternatives for maintaining and restoring prairie. If mowing removes live biomass and prevents sexual reproduction but not vegetative spread, we would expect spatial population structure to correspond to genetic differences found between mowed and burned populations. We then use greenhouse and garden experiments to compare germination and growth among different seed sources and to test seedling growth under different competition and moisture conditions. To further examine factors affecting restoration potential of this species, we compare survivorship and growth of seeds and juvenile milkweeds from different sources planted into native prairie habitats under experimental burning treatments and stochastic climatic variation.

Methods

Study Areas

Studies were conducted at 1 former and 19 current *Asclepias meadii* stations in Kansas, Missouri, Iowa, and Illinois (Table 1). We collected soil samples during 1992 and 1993 from 18 sites, and population data during the 1992 flowering period from 10 sites. These included the fire-managed Rockefeller Prairie and Weimer Hill, both of which were spring-burned in 1992, five annually mowed private Kansas prairie haymeadows, and three Missouri former haymeadows that were protected in the mid 1980s. Two of the Missouri sites are now managed in hay-burn-rest rotations, while flowering

Table 1. Mead's milkweed (*Asclepias meadii*) study sites sampled for soils (S), and for population structure and plant size (P). Two sites were sampled for soils in Ford and Saline counties. See Figure 1 for site locations.

Site number & name	State & county	Samples	Management history
1) Palatine	Illinois/Cook	S	railroad prairie (population destroyed)
2) Ford	Illinois/Ford	S (2)	railroad prairie (two samples)
3) Saline	Illinois/Saline	S (2)	glade/metapopulation (two samples)
4) Woodside	Iowa/Adair	S	haymeadow (mowed in Sep.)
5) Flaherty	Iowa/Clarke	S	preserve
6) Cummings	Iowa/Warren	S	preserve
7) Martensdale	Iowa/Warren	S	preserve
8) Garnett	Kansas/Anderson	P	haymeadow
9) Sunset	Kansas/Anderson	S, P	haymeadow
10) Hinton Creek	Kansas/Bourbon	S, P	haymeadow
11) Colyer	Kansas/Douglas	S, P	haymeadow
12) Jack's	Kansas/Douglas	S	haymeadow
13) Fowler Hill	Kansas/Franklin	S	haymeadow
14) French Creek	Kansas/Jefferson	S, P	haymeadow
15) Rockefeller	Kansas/Jefferson	S, P	former haymeadow (burned every 1–3 yrs. since 1956)
16) Cook Meadow	Missouri/Barton	S, P	haymeadow (unmowed when milkweeds flower since ~ 1990)
17) Niawathe	Missouri/Dade	S, P	former haymeadow (burn/hay/rest rotation since ~ 1980)
18) Weimer Hill	Missouri/Iron	S, P	glade/metapopulation (burned)
19) Paint Brush	Missouri/Pettis	S	former haymeadow (burn/hay/rest rotation since ~ 1980)
20) Wah-kon-Tah	Missouri/St. Clair	P	former haymeadow (burn/hay/rest rotation since ~ 1980)

milkweeds are left unmowed in the third site. Greenhouse and garden studies were conducted at the Morton Arboretum, Lisle, Illinois. Restoration planting experiments were conducted at seven prairie habitats in northern Illinois and northeastern Indiana (Table 2). None of these sites contain native *A. meadii* populations, but all lie within the former range of the species. All sites are protected and managed by prescribed burning. They provide an among-site drainage gradient from dry-mesic to mesic, and a successional gradient from early- to late-successional vegetation (e.g., Betz, 1989; Betz & Lamp, 1989; Bliss & Cox, 1964).

SOIL SAMPLING AND ANALYSIS

Composite soil collections were made from each site by pooling multiple A-horizon samples from milkweed habitat into a 2-quart plastic bag that was transported to the Morton Arboretum Soils Lab, Lisle, Illinois. Soils were refrigerated until shipped for analysis by the A & L Great Lakes Laboratories, Fort Wayne, Indiana. Samples were tested for pH, milli-equivalents cation exchange capacity (CEC), percent organic matter (% OM), and parts per million (ppm) phosphorous (P), potassium (K), magnesium (Mg), and calcium (CA), following methods of Page et al. (1982). Sample sites were ordinated by their soils data on PCORD software (McCune,

1993) using the Bray-Curtis technique (Beals, 1984) with a variance-regression endpoint selection and Euclidean distance measure. Samples also were clustered by their soils data on PCORD using Ward's method with a Euclidean distance measure (Sneath & Sokal, 1973). Sample means and standard deviations were calculated for geographically similar groups.

SAMPLING AND ANALYSIS OF NATURAL POPULATIONS

With one exception, all *Asclepias meadii* sites were sampled from stratified random transects through milkweed populations during their flowering period, when plants can be most easily located (Alexander et al., 1997). Because random placement of plots along transects rarely encountered milkweeds, flowering plants were randomly selected as centers of non-overlapping 10-m² circular plots, in which the numbers of flowering and non-flowering plants were counted. This maximized sampling of flowering plants across sites, and also helped focus plot placement on the clonal ramet clusters of this species. For Rockefeller Prairie, density data were obtained by placing a 10-m² grid over a 2-m²-resolution grid map of milkweed clone locations. At this scale, the comparatively small ramet clusters at Rockefeller (Alexander et al., 1997) were easily quantified within sampling plots. All

Table 2. Location, site characteristics, and number of experimental Mead's milkweed (*Asclepias meadii*) plantings made at Mead's milkweed restoration sites.

Site name	County, state	Size	Drainage/successional stage	Management treatment	Number planted (1994–1996)		
					Seeds	Tubers	Genotypes
Biesecker (Cook)	Lake Co., Indiana	16 ha	dry-mesic/late-succ.	Burned-unburned 1994	201	117	32
Vermont Cemetery	Will Co., Illinois	0.4 ha	mesic/late-succ.	Burned-unburned 1996	196	148	33
Pellville Cemetery	Ford Co., Illinois	0.2 ha	mesic/late-succ.	Burned-unburned 1995	140	93	29
Hickory Creek	Will Co., Illinois	35 ha	dry-mesic/early-succ.	Burned 1994	155	61	28
Schulenberg Prairie	DuPage Co., Illinois	20 ha	dry-mesic/mid-succ.	Burned 1994–1995	201	103	33
Munson Cemetery	Henry Co., Illinois	2 ha	dry-mesic/late-succ.	Burned 1995	243	79	26
W. Chicago Prairie	DuPage Co., Illinois	47 ha	mesic/mid-succ.	Unburned 1995	96	29	24
				Totals:	1232	630	53

ramets sampled were quantified by their reproductive status and size. The extensive vegetative spread of ramets in haymeadows prevented quantifying reproductive status at the genet level. For each flowering ramet, the number of flowers per umbel was recorded. For each plant, the area (length × width) of one randomly chosen leaf from the largest pair of leaves was recorded. This leaf-area was transformed to a plant leaf-area index by multiplying the measured leaf-area for each plant times the number of leaves on the plants.

One-way ANOVA and Duncan's multiple range tests (Steele & Torrie, 1960) were used to compare morphological and population structural differences between fire-managed and mowed populations. The burned Rockefeller and Weimer Hill sites were retained as separate treatments because they occupy ecologically different habitats. To attain similar, but not equal, sample sizes, data were pooled within the Missouri former haymeadows, and within the Kansas current haymeadows. Separate tests were made of the null hypotheses that there were no significant differences between these four groups for mean ramet plot densities, mean percent flowering ramet densities, mean umbel size, mean leaf-area indices of flowering and nonflowering plants, and mean total leaf-area of all *A. meadii* ramets per plot.

GREENHOUSE AND GARDEN EXPERIMENTS

All seeds used in propagation studies were moist-stratified in Petri dishes at 5°C for 4 months before planting in 10-cm-deep flats filled with a mixture of equal parts standard greenhouse soil and prairie loam (Betz, 1989). Seeds were planted in mid May and germinated within 10 days. Flats were retained in the greenhouse until seedlings had developed one pair of leaves, after which they were transferred outside into full sun, which is required for optimum growth (Betz, 1989). Seedling performance was quantified by percent germination for seed pods and seed sources, while performance of older plants was quantified by leaf-area indices after their first year of growth. A one-way ANOVA was used to compare mean percent seed germination of pods from naturally pollinated Rockefeller and Weimer Hill populations against pods derived from garden crosses using geographically distant seed sources.

To assess the effects of grass competition on moisture availability and milkweed seedling growth, we established a drainage gradient among 12 seedling flats (40 seeds/flat), randomly chosen for placement either above (n = 4 flats), midway (n

= 4), or below (n = 4) the level of a 30-cm-deep 1 × 2-m sand bed kept moist by watering. Flats placed below the sand level were expected to have the poorest drainage and highest moisture levels because of capillary movement from the sand bed; elevated flats were expected to have greatest drainage. For each drainage position, two flats were planted with seeds (pooled from multiple pods) obtained by long-distance out-crossing of pollen from natural populations to our garden plants, and two were planted with naturally pollinated seeds pooled from Rockefeller and Weimer Hill pods. After seedling germination, half of the flats in each moisture/seed source treatment were randomly selected and sown with annual oats (*Avena sativa* L., Gramineae). This oat species has similar photosynthetic responses to native prairie grasses such as *Sorghastrum nutans* (L.) Nash (Fay & Knapp, 1993), and its annual growth habit can rapidly develop a fibrous root system that can compete with forb seedlings for water and other resources. The flats were watered periodically to sustain seedling growth, allowing surficial drying between watering periods. We measured the moisture gradient during the growing season by inserting an electrical conductivity moisture meter probe into each flat 24 hrs. after watering. Analog readings ranged from 1 (dry) to 8 (wet). After the milkweed seedlings and oats had become dormant, all seedlings were excavated and their tubers weighed. Effects of the drainage and oats on mean moisture level readings were tested with a fixed model two-factorial ANOVA (Sokal & Rohlf, 1981). Effects of the moisture gradient, oats, and seed sources on mean milkweed tuber weight were measured in a mixed model three-level nested ANOVA (Sokal & Rohlf, 1981) comparing the hierarchical effects of oats, moisture gradient, and seed source by flat.

FIELD ESTABLISHMENT EXPERIMENTS

Experimental plantings of seeds and seedlings were conducted at the seven study sites between 1994 and 1996. Our strategy was to maximize numbers of genetically different individuals within sites so as to increase potential for compatible outcrossing and seed production. This resulted in planting of 1232 seeds and 630 juvenile plants representing 53 different genotypes (Table 2). Milkweed seeds and juveniles were planted in early May prior to the breaking of prairie plant dormancy. Clusters of five seeds were planted 1 cm deep in a 1-dm² area in which the soil was loosened with a hand trowel. One-year-old dormant milkweed tubers were removed from flats, weighed, and packed with sphag-

num in plastic bags for translocation. They were planted upright with buds about 3 cm below the soil surface, in 10-cm-deep incisions made in the prairie with a tile spade. All plantings were watered immediately.

Seeds and tubers were planted within 1-m² plots placed along permanently marked stratified random transects. Usually two seedling clusters and four tubers were planted per plot, and were placed within interstitial patches between bunchgrasses. The transects crossed burned and non-burned sections of Biesecker in 1994, Pellville in 1995, and Munson in 1996, allowing comparison of these management treatments on growth and survivorship. Seedlings were monitored for first-year survivorship, while juvenile plants that emerged from tubers were monitored for survivorship and measured for leaf-area indices. Percent survivorship was determined over time for annual cohorts and compared between seed and tuber plantings. Survivorship was compared between burn and nonburn treatments using Chi-square analysis of 2 × 2 contingency tables, and mean leaf-area indices were compared between the same treatments using t-tests. We also compared differences in mean leaf-area indices among planting sites and seed sources using one-way ANOVAs. A two-way ANOVA was used to compare leaf-area indices between garden and field sites planted with Rockefeller and Weimer Hill seed sources using seeds pooled from multiple pods.

RESULTS

SOIL CHARACTERISTICS

Soil samples ordinated and clustered along a chemical- and nutrient-concentration gradient corresponding to their geographic distribution (Fig. 3). Missouri and southern Illinois sites had the lowest scores on the first axis, Kansas sites were intermediate, and Iowa and northern Illinois sites had the highest scores. All soil variables were positively correlated with the first axis, with CEC, and ppm Mg, K, and Ca having correlations greater than 0.5. In general, Missouri and southern Illinois sites are acid and nutrient-poor, Kansas sites are intermediate, and Iowa and northern Illinois sites are calcareous and nutrient-rich (Table 3). Missouri and southern Illinois had comparatively low mean pH, % OM, CEC, and ppm Ca, but comparatively high ppm P. Kansas samples were generally intermediate but variable, with comparatively high mean pH, low mean % OM, intermediate CEC, and extremely low ppm P. Iowa and northern Illinois had the highest mean values for all soil variables.
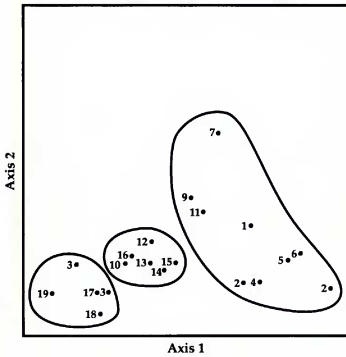
Figure 3. Bray-Curtis ordination of Mead's milkweed (*Asclepias meadii*) habitats by soils characteristics. Axis 1 represents a geographic gradient with increasing pH, % OM, CEC, and nutrient concentrations (see Table 3). Circles are clusters produced by Ward's method. Number codes: northern Illinois (1–2), southern Illinois (3), Iowa (4–7), Kansas (9–15), Missouri (16–19). See Table 1 for site names and Figure 1 for site locations.

SITE-MANAGEMENT EFFECTS ON POPULATION STRUCTURE

Asclepias meadii ramet densities were significantly higher in Kansas haymeadows than in Rockefeller Prairie, and were intermediate in the former Missouri haymeadows and Weimer Hill (Table 4). At Rockefeller and Weimer Hill, 68% of all ramets were flowering, while only 18.6% of all plants flowered in haymeadows. On a plot basis, the percentage of flowering ramets averaged under 32% in Kansas and former Missouri haymeadows, but more than 60% at Weimer Hill and more than 80% at Rockefeller (Table 4). As a result, the density of flowering plants, but not nonflowering plants, was similar across all study sites and there was no significant difference in mean plot leaf-area across all sites (Table 4). However, flowering ramets were larger than nonflowering ramets across all sites, and Rockefeller plants were larger than haymeadow plants in flowering and nonflowering groups (Table 4). Flowering plant umbels were larger in burned habitats, averaging about 12 flowers, and had about 10 or fewer flowers in Kansas and former Missouri haymeadows (Table 4).

GREENHOUSE AND GARDEN EXPERIMENTS

Between 1993 and 1996, seed production among our garden plants averaged 56 seeds/pod, which

Table 3. Geographic differences in mean (± s.e.) soil chemistry values and nutrient concentrations of habitats supporting extant or former Mead's milkweed (*Asclepias meadii*) populations. See Figure 1 and Table 1 for location and description of sample areas.

Region	Sample size	Community	% OM	CEC	pH	ppmP	ppmK	ppmMg	ppmCa
N. Illinois & Iowa	7	Prairie	11.09 ± 4.00	20.64 ± 3.27	6.67 ± 0.82	6.71 ± 3.27	229 ± 87.88	412.86 ± 108.85	2992.9 ± 921.7
Kansas	7	Prairie/Haymeadow	5.54 ± 0.96	15.27 ± 3.48	6.47 ± 0.77	1.71 ± 1.25	75.43 ± 41.69	255 ± 38.19	2200 ± 754.43
Missouri & S. Illinois	6	Haymeadow/glade	5.05 ± 1.97	6.30 ± 2.24	5.67 ± 0.85	6.67 ± 1.25	73.0 ± 23.43	116.67 ± 34.74	738.33 ± 530.49

Table 4. Site management effects on mean ramet and mean percent flowering ramet density per 10-m² plot, mean umbel size, mean leaf-area index, and average plot leaf-area of Mead's milkweed (*Asclepias meadii*) in burned prairies (Rockefeller and Weimer Hill), former haymeadows (Missouri), and current haymeadows (Kansas). Similar lower case letters indicate similar means across variables with Duncan's multiple range test at P = 0.05.

Variable	Rockefeller	Weimer Hill	Missouri prairies	Kansas haymeadows	Test statistic and probability
Mean ramet density ± s.e.	2.525a ± 0.31 n = 40	3.625ab ± 0.84 n = 8	4.6ab ± 1.3 n = 15	6.15b ± 0.91 n = 34	$F = 5.16, P = 0.0024$
Mean % flowering ramet density ± s.e.	80.07a ± 4.87 n = 40	67.26a ± 9.12 n = 8	26.05b ± 9.0 n = 15	31.29b ± 5.40 n = 34	$F = 19.71, P < 0.0001$
Mean flowers per umbel ± s.e.	11.89abc ± 0.35 n = 73	12.40ab ± 1.15 n = 15	9.27cd ± 0.65 n = 11	10.09bcd ± 0.52 n = 45	$F = 4.68, P = 0.0038$
Mean leaf-area index of flowering plants ± s.e.	196.09a ± 8.03 n = 73	162.33 ab ± 27.75 n = 15	137.52b ± 27.13 n = 11	142.89b ± 12.4 n = 45	$F = 54.71, P < 0.0001$
Mean leaf-area index of nonflowering plants ± s.e.	138.54a ± 10.85 n = 73	92.36b ± 17.76 n = 15	37.64c ± 4.93 n = 11	73.29b ± 4.59 n = 45	$F = 15.89, P < 0.0001$
Mean plot leaf-area ± s.e.	453.86 ± 78.55 n = 37	551.70 ± 106.85 n = 8	243.81 ± 56.34 n = 15	605.42 ± 118.18 n = 33	$F = 1.74, P = 0.165$

was similar to the 60 seeds/pod average found by Betz (1989) from 1965 to 1971 for native plants in Missouri and Kansas railroad prairies. Under greenhouse conditions, 74.3% of 1665 seeds germinated. Also with greenhouse propagation, there was no significant difference ($F = 0.78$, $P = 0.4679$) in mean percent germination per pod among our wild-collected seed from Weimer Hill ($n = 11$ pods, $\bar{x} = 60.73 \pm 10.3$), Rockefeller Prairie ($n = 11$ pods, $\bar{x} = 71.12 \pm 8.4$), and pods derived from garden crosses among geographically different seed sources ($n = 17$ pods, $\bar{x} = 74.65 \pm 6.4$). Four life-stage classes could be recognized in garden-propagated plants: first-year seedlings (< 15 cm high, < 5 cm long linear leaves), second-year juveniles (> 15 cm high, 1 × 5 cm lanceolate leaves), and flowering or nonflowering adults (> 30 cm high, > 1 cm broad lanceolate-sagittate leaves with cordate bases). In the field, ramets of adults can revert to juvenile form in successive years (Betz, 1989).

The presence of oats significantly reduced soil moisture levels in milkweed flats, reversing the relationship between moisture level and drainage sequence (Table 5). Overall moisture levels were higher in flats without oats, where the highest drainage position had the lowest mean moisture level. With oats, the moisture gradient was reversed, with a higher mean moisture level at the highest drainage position. Although drainage position did not affect tuber weight ($F = 0.0974$, $P = 0.9095$), the presence of oats significantly reduced the overall mean weight of milkweed tubers, with differences between seed sources (Table 5). Oats reduced the mean weight of tubers from the natural Rockefeller and Weimer Hill seed sources, but not the mean weight of tubers produced by garden outcrosses among geographically distant seed sources.

FIELD ESTABLISHMENT EXPERIMENTS

By the end of 1996, 332 seedlings and 290 juveniles representing 46 genetically different individuals had been established at the seven study sites. Significant variation in the germination, survivorship, and growth of these plants was caused by weather, fire, and differences among seed sources.

Although greenhouse seed propagation rates were stable in 1994–1996, seedling survivorship in the field was 11% or less in 1994 and in 1995, but increased to more than 40% in 1996 (Fig. 4). This difference in survivorship corresponded to below-normal May–July rainfall in 1994–1995 and an above-normal May–July rainfall (200% of normal)

Table 5. Experimental effects of artificial drainage gradient position and presence or absence of oats (*Arena sativa*) on mean moisture levels (conductivity), and effects of presence or absence of oats and seed source (natural within-population crosses vs. artificial long-distance outcrosses) on mean weights of Mead's milkweed (*Asclepias meadii*) tubers. Drainage gradient position: high = greatest elevation and drainage, mid = intermediate elevation and drainage, low = lowest elevation and drainage. Oats' effect on moisture level: $F = 75.58$, $P < 0.0001$; drainage effect on moisture level: $F = 2.39$, $P = 0.0931$; oats × drainage interaction: $F = 9.03$, $P = 0.0001$. Oats' effect on tuber weight: $F = 5.656$, $P = 0.035$; seed source effect on tuber weight: $F = 4.75$, $P = 0.0001$.

| | Mean moisture level (conductivity) ± s.e. | | | Mean tuber weight ± s.e. in grams | |
| | Gradient position | | | Seed source | |
	high $n = 40$	mid $n = 40$	low $n = 40$	within-population $n = 90$	long-distance $n = 90$
Oats present	3.25 ± 0.19	2.40 ± 0.14	2.54 ± 0.18	0.219 ± 0.010	0.272 ± 0.011
Oats absent	4.62 ± 0.19	5.28 ± 0.22	5.83 ± 0.20	0.338 ± 0.0125	0.326 ± 0.013

in 1996, which enhanced seed germination and seedling survival. Seedling cohort survivorship over time was low, dropping to about 10% after two or three growing seasons; a few seeds delayed germination until the second growing season, causing the upward deflection of the 1994 survivorship curve in 1996 (Fig. 5). Survivorship of planted tubers was higher, with 50% or more of these cohorts alive after two or three growing seasons (Fig. 5). Differences among four planting sites also significantly

affected sizes of three-year-old plants, as measured by leaf-area index ($F = 21.53$, $P < 0.0001$). Plants with the largest mean leaf-area occurred in the Vermont Cemetery and averaged twice the size of plants at Biesecker Prairie. Plants at the Schulenberg and Hickory Creek sites were intermediate in size.

Prescribed burning had either positive or neutral effects on seedling and tuber survivorship and leaf-area in all three study sites (Table 6). Two years
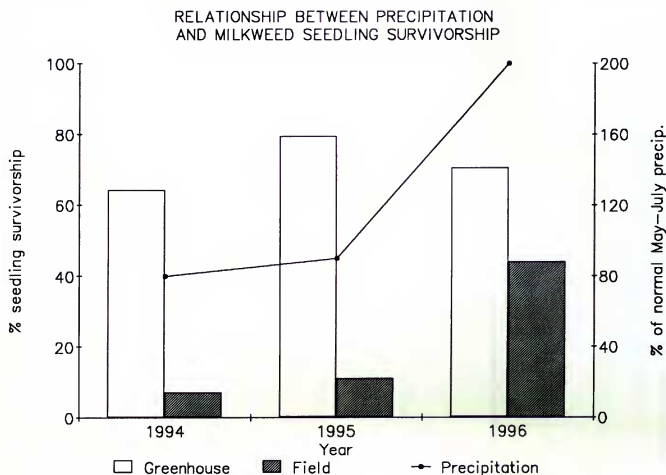

RELATIONSHIP BETWEEN PRECIPITATION
AND MILKWEED SEEDLING SURVIVORSHIP

Figure 4. Temporal relationship between percent of normal May–July precipitation and first-year survivorship of greenhouse- and field-germinated Mead's milkweed (*Asclepias meadii*) seedlings. Precipitation levels are northeastern Illinois summaries from the National Oceanic and Atmospheric Administration.
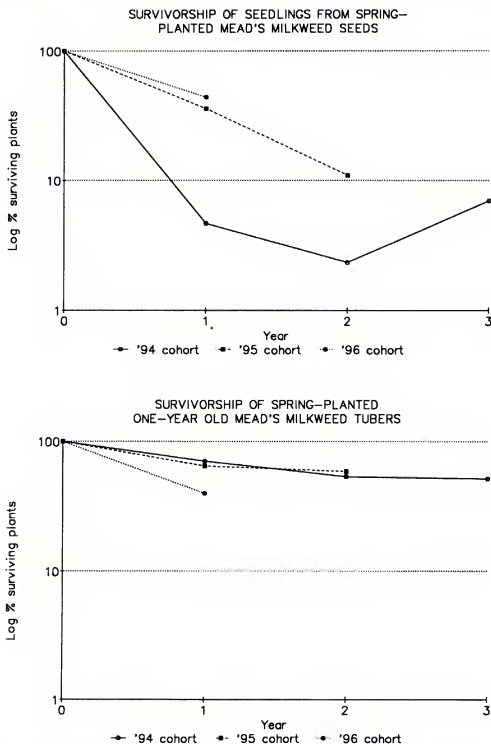
Figure 5. Cohort survivorship curves for spring-planted Mead's milkweed (*Asclepias meadii*) seedlings (upper) and tubers (lower) at seven northeastern Illinois and Indiana restoration sites.

after the burn at Biesecker Prairie, seedling survivorship did not differ significantly between treatments, but tuber survivorship and mean leaf-area index were greater in the burn treatment. One year after the burn at Pellville, seedling survivorship and tuber leaf-area did not differ significantly, but tuber survivorship was greater in the burn treatment. At Munson, only seedling survivorship was significantly greater in the year of the burn. The overall lower survivorship of tubers in 1996 may have been caused by excessive handling and storage. After these plants were excavated from flats and weighed, they had to be held in cold storage

for about a month before planting due to a late cold spring.

In the garden versus field comparison of performance between Rockefeller and Weimer Hill seed sources, garden-grown plants had significantly larger mean leaf-area indices than field plants (F = 363.78, $P < 0.0001$). After three years, most field plants had reached the size of second-year juvenile garden plants, while garden-grown plants had attained an adult size. Averaged across both planting treatments, Weimer Hill plants were larger than Rockefeller plants (F = 85.09, $P < 0.0001$). There was also a significant site × seed source interaction

Table 6. Effects of prescribed burning on Mead's milkweed (*Asclepias meadii*) seedling and tuber survivorship and mean leaf-area indices in three restoration plantings. Survivorship *P* values are based on Chi-square contingency tables. Leaf-area index *P* values are based on Student *t*-tests.

Variable	Site/planting date					
	Biesecker/1994		Pellville/1995		Munson/1996	
	Burned ('94)	Unburned	Burned ('95)	Unburned	Burned ('96)	Unburned
Seedling (*N*) survivorship (1996)	18	15	30	25	49	50
	17% ($P < 0.825$)	13%	13% ($P = 0.844$)	8%	59% ($P = 0.057$)	38%
Tuber (*N*) survivorship (1996)	41	39	14	15	39	40
	83% ($P < 0.001$)	51%	86% ($P = 0.013$)	33%	41% ($P = 0.216$)	58%
Leaf-area (*N*) index ± s.e. (1996)	41	39	14	15	39	40
	25.51 ($P = 0.006$) ± 2.23	14.08 ± 2.09	16.54 ($P = 0.636$) ± 1.74	14.59 ± 2.91	4.42 ($P = 0.467$) ± 0.64	5.14 ± 0.68

($F = 83.28$, $P < 0.0001$); Weimer Hill plants had more than twice the leaf-area of Rockefeller plants in garden, but not in field, habitat. Overall tuber weight also had a significant ($P < 0.0001$) but small ($r^2 = 0.18$) positive correlation with leaf-area index for field-planted milkweeds in 1996. Excessive handling and storage may have reduced this correlation.

DISCUSSION

IMPLICATIONS OF HABITAT DIFFERENCES AND GENETIC VARIATION

Despite the apparent lack of allozyme differentiation across its range (Tecic et al., 1998), *Asclepias meadii* occupies a strong geographic gradient in soil characterisitics, which have been found to affect allozyme frequencies in some species (e.g., Heywood & Levin, 1985). Our initial success in restoring plants from Missouri and Kansas seed sources into the nutrient-rich soils of northern Illinois also suggests that these soil differences may not be critical to *A. meadii*. It is unknown if size differences in garden habitat between plants from these seed sources reflect an important fitness component, or simply phenotypic variation associated with genetically diverse plants under noncompetitive conditions. Certainly, they were not expressed in the field, where competitive stress should make differences that reflect fitness more apparent. In Pitcher's thistle (*Cirsium pitcheri* Torr., Compositae), a monomorphic species with little geographic allozyme variation, plants from Wisconsin and Indiana seed sources differed in seedling morphology in the greenhouse, and in subsequent survivorship and growth when planted in an Illinois restoration (Bowles et al., 1993b; Bowles & McBride, 1996).

When plants from geographically distant seed sources are integrated in restorations and cross-pollinate, the potential exists for disruption of naturally evolved lineages and outbreeding depression caused by breaking up locally co-adapted gene complexes (Fenster & Dudash, 1994). The breeding system, pollen packaging as pollinia, and strongly-flying pollinators of milkweeds may contribute to usually large neighborhood sizes (Broyles & Wyatt, 1991; Wyatt & Broyles, 1994), which could select against deleterious effects of outcrossing. This may vary among milkweed species. For example, Wyatt (1976) found greater percent fruit set from within-population crosses of *A. tuberosa* in comparison to between-population crosses across a wide geographic region, suggesting outbreeding depression. However, our failure to find differences in percent seed germination between natural and geographically distant crosses suggests that outbreeding may not be a critical factor for *A. meadii* at this early life-stage. In our garden experiment, seedlings from distant crosses developed larger tubers than seedlings from natural populations when grown in competition with oats, and the larger plants correlated with greater plant size when outplanted the following year. This apparent heterosis effect could outweigh deleterious consequences of long-distance crosses (Fenster & Dudash, 1994). Additional studies are needed to assess the survivorship and growth of seedlings and backcrosses from geographically distant sources to determine if population viability is negatively affected.

In addition to total lack of reproduction, small populations of self-incompatible plants can undergo rapid increases in inbreeding, which could be detrimental to population growth in restorations

(DeMauro, 1993). For *A. meadii*, inbreeding depression could be a serious problem, but we have only circumstantial evidence. For example, our three-year 75% greenhouse germination rate was significantly greater ($X^2 = 280.6$, $P < 0.001$) than the 47.6% germination found by Betz (1989) for 2429 wild-collected seeds. This lower germination may have been caused by inbreeding in the isolated linear railroad prairie populations that Betz studied. In contrast, our seed collections were either from populations known to be genetically diverse or from controlled garden crosses. Although inbreeding may reduce seed production, inbreeding-induced differences in fitness in plant species may be expressed under stressful field conditions and at different life stages depending upon their breeding systems (Dudash, 1990; Fenster & Dudash, 1994; Carr & Dudash, 1996). Further greenhouse and field studies are needed to assess inbreeding effects in *A. meadii*.

HABITAT MANAGEMENT EFFECTS

Prescribed burning and mowing appear to have different effects on population structure of *Asclepias meadii*. The greater leaf-area of flowering milkweeds at Rockefeller and the larger umbel sizes and greater percentage of flowering plants in burned sites suggest that these plants are placing more resources into the potential for sexual reproduction than are plants in haymeadows. For example, although the smaller ramet and flower sizes of haymeadow plants could reflect stress from summer mowing, the greater ramet densities but similar average plot leaf-area in Kansas haymeadows suggest a reallocation of resources into vegetative spread due to lack of sexual reproduction. However, this vegetative spread appears to accompany the loss or attrition of genetically different individuals, which would limit sexual reproduction in this self-incompatible species (Tecic et al., 1998). In comparison, the greater diversity of genotypes in burned areas would facilitate more successful cross-pollination among sexually compatible plants. The Missouri populations on former haymeadows had a comparatively low, although not significantly different, mean plot leaf-area, which does not strongly support our resource reallocation hypotheses. Population structure at these sites could be responding to the novel effect of reduced mowing frequency, which may contribute to loss of genetically similar ramets once annual mowing was stopped.

Fire is a natural factor responsible for maintenance of prairie, with varying effects on individual

plant species (Collins & Glenn, 1988; Collins & Gibson, 1990; Evans et al., 1989; Collins & Wallace, 1990). *Asclepias meadii* appears to be fire-adapted. Betz (1989) found 77.1% flowering stems in annually burned prairies in railroad rights-of-ways, and greater flowering occurs in years of prescribed burns at Rockefeller Prairie (H. M. Alexander, pers. comm.). This is reinforced by our finding of increased milkweed juvenile growth and survivorship in burned tracts. Because of the low annual fruit production and seed production in this species (Betz, 1989; Alexander et al., 1997), fire may be critical for long-term population maintenance and could accelerate restored population growth.

POPULATION DEMOGRAPHY

The slow growth of restored milkweeds and lack of sexual reproduction after three years extremely limits demographic interpretations during this period. Seedling survivorship was essentially less than 10% for the first two cohorts, and no seedling plants attained the sizes reached by second-year juveniles in garden plots. The 40% seedling survivorship in 1996 should allow greater second-year survivorship of this cohort, but development into a juvenile or reproductive state may require many years under field conditions. There also have been few transitions from juvenile to reproductive states. For example, 5% of all plants flowered in 1995, but fewer plants flowered in 1996, and only two plants flowered in both years. Also, none of these plants have produced seed pods, either due to lack of pollination or compatible crosses, or to inability to allocate enough resources to produce pods.

Guerrant (1996) suggested that a restoration strategy of using outplanted juveniles rather than seeds would increase survivorship and population growth. Our preliminary data also indicate that initiating a milkweed population with planted juveniles can reduce mortality rates and accelerate development of larger population sizes. However, garden propagation increases chances of recruiting less fit plants that might not survive selective pressures that operate at the seedling stage. Planting of seeds is required to help assess if plants can actually complete their life-cycles, but this necessitates a longer restoration process with higher mortality rates and greater seedling vulnerability.

ENVIRONMENTAL EFFECTS ON DEMOGRAPHY

Demographic monitoring of the trends of restored population growth can be enhanced by resolution of critical factors affecting reproduction, survivor-

ship, and growth (Pavlik, 1994). Three environmental factors—moisture levels, competition, and site variation—appear to have important effects on population establishment and growth of *Asclepias meadii*. DeMauro (1994) found higher seedling recruitment of *Hymenoxys acaulis* (Pursh) K. L. Parker var. *glabra* (A. Gray) K. L. Parker (Compositae) during years without summer drought. We also found that growing season rainfall strongly influenced the fate of field-planted seeds, with survivorship exceeding 40% only in 1996, when rainfall exceeded 200% of normal. This suggests that recruitment into natural populations is uncommon and rainfall-dependent, providing a selective requirement for longevity of adult plants. As a result, lack of growing-season rainfall could negatively impact demographic processes when restoring populations from seed. Competition from grasses, with their fibrous root systems, can negatively affect forb survivorship and growth (Gurevitch, 1986; Louda et al., 1990; Hook et al., 1994). As expected, oats significantly reduced milkweed growth, apparently through competition for moisture. This indicates that competition from existing prairie grasses should slow plant growth and delay transition of cohorts into adult stages. *Asclepias meadii* may be adapted to the bunch-grass structure of late-successional prairie by an ability to establish in patches between grasses, and by using its longevity to persist in this competitive but stable environment. The highly significant difference between garden and field effects on milkweed growth also indicates the high level of competition in field habitats. Greenhouse-propagated plants often flower and may produce pods in three years. But, as indicated, few field-planted milkweeds have flowered, and seedlings from planted seeds still resembled first-year greenhouse seedlings after three years. However, significant differences in growth between different sites indicate that a wide range of conditions affecting plant growth exist in field habitats. For example, the greater size of plants restored at Vermont Cemetery may correlate with its lower landscape position and greater moisture retention compared with other, more well-drained restoration sites.

Our results also suggest that burning should accelerate demographic processes by increasing seedling survivorship and growth of plants. However, weather cycles such as drought may override positive effects of fire, as different precipitation levels clearly affected seedling establishment over time. Although optimum seedling growth for *A. meadii* is in full sun (Betz, 1989; Bowles, pers. obs.), seedling survival requires adequate moisture that could be retained longer in soils under unburned vegetation.

These factors also would be affected by site drainage, exposure, and soil water-holding capacity. Burned mesic habitat may have optimum germination but strong late-season grass competition. Dry-mesic habitat may have less competition but stronger moisture requirements for seedling establishment. Because weather is unpredictable, experimental burn and non-burn treatments appear necessary for milkweed establishment when supplemental watering is unavailable. Summer mowing may have some benefit in restoring *A. meadii* if it increases ramet numbers, possibly through decreased competition from warm-season grasses. However, we have no data on the effects of mowing on seedling recruitment, and long-term repeated mowing appears to cause genetic attrition (Tecic et al., 1998).

SUMMARY AND CONCLUSIONS

Pavlik (1996) identified proximal (completion of life-cycle, cohort replacement, and population increase) and distal (attainment of Minimum Viable Population) restoration objectives for plants. Restoration of *Asclepias meadii* is clearly in the proximal stage, and the time scale for even short-term success of this late-successional species is unknown. These small populations remain vulnerable to impacts from stochastic demographic or environmental events that could eliminate all or a large proportion of their plants (Menges, 1991, 1992), and their effective population size (N_e) is controlled by their outcrossing mating system, which requires crossing with different genotypes. A realistic short-term goal should be establishment of the number of genotypes present in natural populations. Allozyme sampling found 27 genotypes in the Weimer Hill population, and 15 genotypes at Rockefeller (Tecic et al., 1998), and over 200 genetically different plants actually may be present at Rockefeller (Alexander et al., 1997). To restore large numbers of genotypes will require mixing geographically different seed sources. Such crossing has the potential for disrupting locally adapted lineages and causing outbreeding depression, but the unusually large neighborhood sizes of milkweed species may buffer them from these genetic effects. Although our preliminary success with planting of Missouri and Kansas milkweed seedlings into northern Illinois habitats supports this hypothesis, additional work is needed to understand long-term consequences.

Additional constraints on the development of large milkweed populations are related to problems of size or scale (White, 1996). *Asclepias meadii* is so uncommon within natural habitats that it is rare-

ly encountered by random sampling, and its apparent requirement of late-successional vegetation currently limits restoration to small sites, because no large sites exist in the eastern part of its range. Restoration of larger high-quality prairies is also not a short-term process, and has not been attained even after 20 years (Schramm, 1992). As a result, habitat size may regulate population growth by limiting effective population size and reproductive potential, and by enhancing inbreeding effects. Development of an inordinately large or dense population within a small area could result in density-dependent disease or insect infestations that would have disastrous effects on populations. For example, severe damage, and possibly mortality, to *A. meadii* can be caused by milkweed cerambycid beetles (*Tetraopes* sp.) and by milkweed weevils (*Rhyssematus* sp.). The adult *Tetraopes* feed on leaves and flowers, while their larvae feed on roots. *Rhyssematus* grubs feed on milkweed pith, which may weaken the stem, while adults may topple the terminal umbel, thereby preventing seed production (Betz, 1989; R. F. Betz, pers. obs.).

Managing fragmented *A. meadii* restorations as metapopulations may help resolve the population size dilemma. The transferring of genetic material among sites could maintain a high level of genetic variation across restorations (Lacy, 1987, 1994; Tecic et al., 1998). This would help provide demographic stability by enhancing outcrossing potential while avoiding problems otherwise associated with high densities of small populations.

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